

Report

Collapse of a New Living Species of Giant Clam in the Red Sea

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Summary

Giant clams are among the most spectacular but also the most endangered marine invertebrates. Their large size and easy accessibility has caused overfishing and collapse of the natural stocks in many places and local extinction in some of the species [1, 2]. The diversity of giant clams is extremely low because of reliction in this Tethyan group [3, 4]. The latest additions of living species date back almost two decades [5–7], fixing the number of extant *Tridacna* at seven species [3]. Here, we report the discovery of a new species of giant clam: *Tridacna costata* sp. nov. features characteristic shells with pronounced vertical folds, is genetically distinct, and shows an earlier and abbreviated reproduction than its Red Sea congeners. This species represents less than 1% of the present stocks but up to >80% of the fossil shells. The decline in proportion and shell size (20×) indicates overharvesting [8] dating back to the early human occupation of the Red Sea >125,000 years ago [9]. This earliest depletion reported so far of a shallow-water megafaunal invertebrate has important ramifications for human dispersal out of Africa [10]. Its oversight in one of the best-investigated reef provinces [11–13] illustrates the dearth of knowledge on marine biodiversity.

Results and Discussion

Morphology has been the foundation of taxonomy for centuries but has often failed to delineate between species with

overlapping and variable phenotypes. The incorporation of molecular and ecological data has greatly sharpened our ability to draw species boundaries and to arrive at a more realistic upward revision of biodiversity by using an integrative taxonomy approach [14]. *Tridacna maxima* Röding 1798 is the most wide-ranging and morphologically variable of the giant clam species [15]. Although different phenotypes were erroneously described as different species resulting in a high number of synonyms [15], the plasticity may, on the other hand, have hampered the recognition of true species boundaries.

Here we provide evidence for a morphologically, genetically, ecologically, and paleoecologically distinct new species of *Tridacna* in the Red Sea.

Tridacna costata sp. nov. features a deeply folded, almost zig-zag dorsal shell margin (Figure 1A; Figure S1 available online), reminiscent of the distantly related *T. gigas*. This character allows for an easy distinction from the two Red Sea congeners, the fluted clam (*T. squamosa* Lamarck 1819) and *Tridacna maxima* Röding 1798. The latter two species show only weakly sinusoidal dorsal shell margins (Figure 1B). We quantified the morphological similarities by five morphological parameters (Figure 2A). Analysis of similarity (ANOSIM) [16] showed a highly significant separation of *T. costata* from the other two Red Sea species ($p < 0.001$), illustrated in three distinct clusters of the multidimensional scaling (MDS) plot [16] (Figure 2A), which demonstrates that *T. costata* is not a cryptic but an overlooked overt species.

The morphological differences were corroborated by phylogenetic analysis of molecular data. With a 415 bp fragment of the mitochondrial 16S rRNA gene, we found a clear delineation between *T. costata* and its sympatric congeners, but virtually no difference between replicate specimens, supporting monophyly of *T. costata* (bootstrap values $\geq 98\%$; Figure 2B). The same genetic distance was evident between *T. costata* and *T. maxima*, as between the sister species *T. squamosa* and *T. crocea* (Table S1), supporting the conclusion that *T. costata* is a new species. Phylogenetic analysis supports the inclusion of the new species along with *T. maxima*, *T. squamosa*, and *T. crocea* in the subgenus *Chametrachea* [17].

Although seasonal times of reproduction are not diagnostic features per se and may vary between years and regions, we found marked differences between the Red Sea species, underscoring the morphological and genetic results: *Tridacna costata* differed from its Red Sea congeners in an early and only brief reproductive period in spring (Figure 2C) coinciding with the seasonal plankton bloom [18]. The timing of reproduction along with the small diameter of the ova (75 ± 2 [SEM] μm) suggests a planktotrophic development of the larvae [19], contrasting the lecithotrophic and hence food-independent larval development in the summer-spawning *T. squamosa* and *T. maxima* with much larger eggs ($35\% \pm 1\%$ and $41\% \pm 2\%$ by volume, respectively).

No significant differences were found in either zooxanthellae clades or photosynthetic performance between *T. costata* and *T. maxima*, whereas *T. squamosa* specimens harbored different symbionts (Figures S2 and S3).

Underwater surveys carried out in the Gulf of Aqaba and northern Red Sea showed that *T. costata* must be considered

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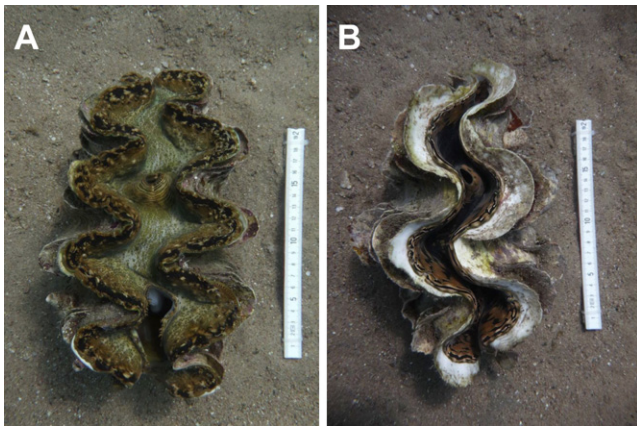


Figure 1. Photographs of Giant Clams
Live (A) *Tridacna costata* and (B) *Tridacna squamosa* from the Red Sea.
Scale bar represents 20 cm. Photo courtesy M. Naumann.

critically endangered by the IUCN categories and criteria for red-listed species [20]. Only six out of a thousand live specimens belonged to the new species, with densities averaging 0.9 ± 0.4 individuals per 1000 m². Highest numbers occurred on offshore shoals in the Red Sea proper but adult broodstock was below detection in much of the investigation area (Figure 3A). Overall, *Tridacna* stocks have plummeted to less than 5% of their sizes in the 1980s and 1990s ($0.1\text{--}1.6$ ind. m⁻²) [21, 22] because of artisanal reef-top gathering for meat and shells [23]. As opposed to *T. maxima* and *T. squamosa*, which have a broad vertical range of distribution, *T. costata* is restricted to the reef top (Table S2). Live specimens were found exclusively in very shallow water. The restricted vertical range, along with its narrow reproductive window and plankton-dependent larval development, make *T. costata* particularly vulnerable to overfishing [24].

We carried out surveys along the shores and well-dated emerged reef terraces of Sinai [25] and Aqaba [26, 27] showing that *T. costata* constituted >80% of giant clam stocks prior to the last interglacial (122,000 to 125,000 years ago), after which its proportion plummeted to <5% in freshly discarded shell middens (Figure 3B, stacked bars). Although natural disturbances, including catastrophic low tides [28] and orbital time-scale changes in Red Sea productivity [26] may have caused differential rates of recruitment and mortality between the three Red Sea species, the dramatic reduction in *Tridacna* size (Figure 3B, lines), equivalent to a ~20-fold decrease in individual body mass and fecundity accompanying the species shift, strongly suggests overfishing [8] (see Supplemental Data). This is corroborated by marked size differences between harvested and unharvested *Tridacna* populations in protected areas [23].

The wealth of paleolithic artifacts in emerged reef terraces in the southern and central Red Sea indicates that modern humans have been exploiting Red Sea mollusks for at least 125,000 years [9, 29]. Although the southern biogeographical boundary of *T. costata* is so far unknown, shells matching our description were also among the fossils in other Red Sea areas [30], suggesting that the new species, by virtue of its dominance, conspicuousness, size, and accessibility, has played an important role in the diet of human gatherer communities during the last interglacial. Along with early shellfishing

evidence in other areas [31], this has spurred speculation that the dispersal of anatomically modern humans out of Africa into the Red Sea and adjacent regions 110,000 to 90,000 years ago [32] was driven largely by competition for marine resources [10]. Our discovery that *T. costata* was already on a trajectory of decline prior to this period corroborates this hypothesis, by providing the first circumstantial evidence that humans were not only using but also depleting reef resources, marking *T. costata* the likely earliest victim of anthropogenic degradation of coral reefs [8, 24]. Declining marine and terrestrial resources, by human and climatic factors, respectively, may have acted in concert to thwart the precocious but short-lived colonization of the Near East by anatomically modern but technologically primitive humans at the end of the last interglacial [32].

Systematics

We propose the following classification for the new living species of giant clam.

Class: Bivalvia Neumeyer, 1884; subclass: Heterodonta Neumeyer, 1884; order: Veneroida Rafinesque, 1815; superfamily: Tridacnoidea Lamarck, 1819; family: Tridacnidae Lamarck, 1819; subfamily: Tridacninae Lamarck, 1819; genus: *Tridacna* Bruguière, 1797; subgenus: *Chametrachea* Mörch, 1853; species: *Tridacna costata* Roa-Quiaoit, Kochzius, Jantzen, Zibdah, Richter sp. nov.

Etymology

The species name (from Latin *costatus*, -a, -um for ribbed) reflects the main diagnostic feature—the shell's narrow rib-like vertical folds.

Holotype

The complete holotype specimen (length, 32.0 cm; height, 19.6 cm; width, 17.2 cm) was collected on 18 February 2006 by H. Roa-Quiaoit and Y. Ahmed in the southern reef flat of the Marine Reserve of the Aqaba Marine Science Station, Jordan, Gulf of Aqaba (29°30' N, 34°34' E, Red Sea) at the Aqaba Marine Science Station in Jordan, Reg. No. 0001 (Figure 4). The soft body parts were preserved in 4% buffered formalin.

Paratype and Synonymies

The scarcity of live specimens—only 13 individuals along the entire Jordanian Red Sea coast—prohibited collection of paratypes. Shells, drawings, and photographs from non- or misidentified specimens are among the material of historical collections and in the scientific literature [30]. None of the synonymies listed by Rosewater [15] for the Red Sea congeners *T. squamosa* and *T. maxima* correspond to the description of *T. costata*.

Locality and Habitat

The species occurs throughout the Red Sea area investigated in this study: northeastern Gulf of Aqaba (type locality); Sinai coast, western Gulf of Aqaba; northern Red Sea, Egyptian mainland down to Hurghada (Figure 3A) and Safaga. Live specimens were found exclusively in very shallow water including reef flats, seagrass beds, sandy-rubble flats, on slight depressions in barren rocky flats, or under branching corals or coral heads, shallower than 2 m (Table S2). All clams were weakly attached to the substrates.

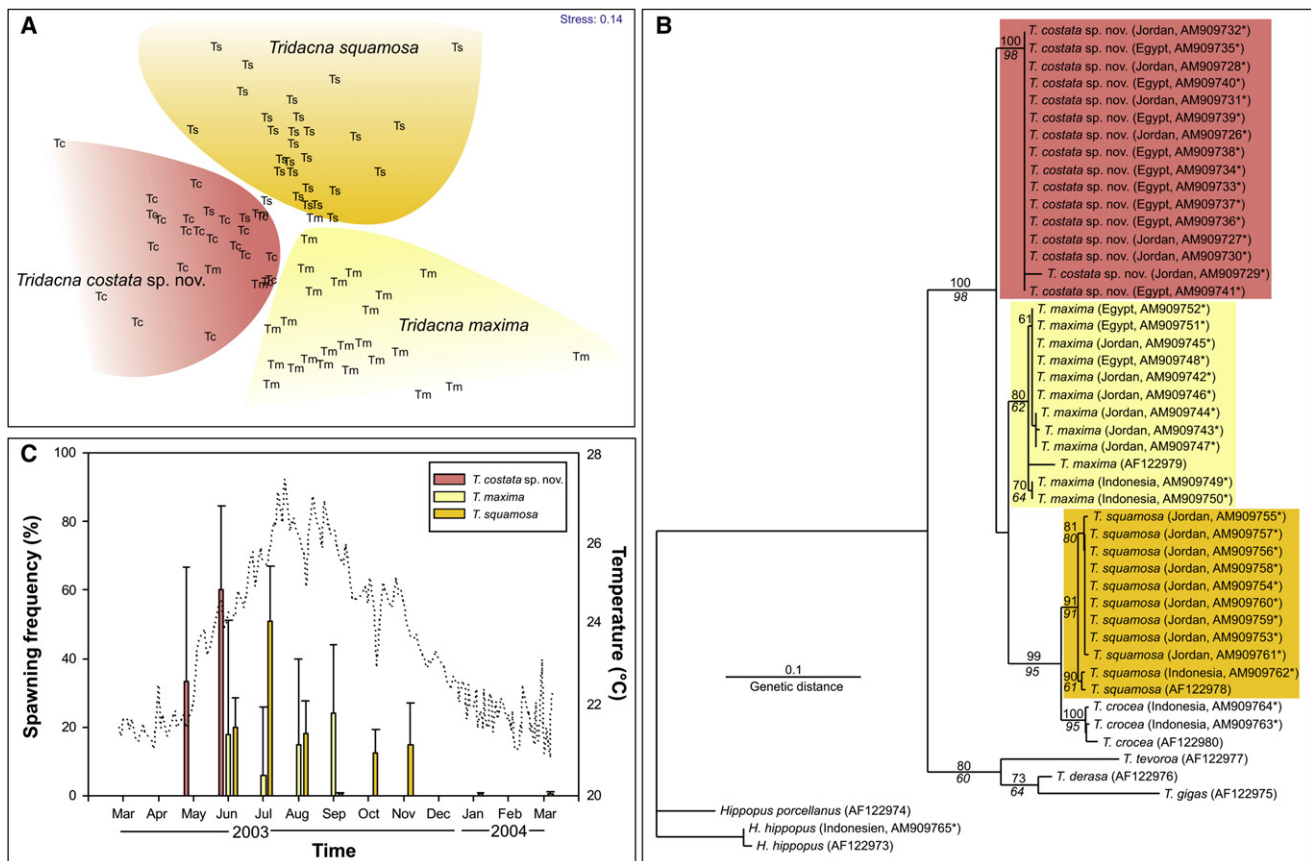


Figure 2. Analyses of Morphological, Genetic, and Ecological Similarities

(A) MDS plot [16] based on normalized Euclidean distances between Red Sea *Tridacna costata*, *T. maxima*, and *T. squamosa* in the ratio of shell length to shell height, shell weight, hinge length, pedal length, and relative umbo position ($n = 30$ ind. each; see Figure S1 for shell parameters). Stress factor indicates useful projection.

(B) Neighbor-joining (NJ) tree of partial 16S rDNA sequences (415 bp) from all extant giant clams available. Numbers above branches indicate bootstrap values for NJ, italic numbers below branches bootstrap values for maximum parsimony (MP) analysis (both 1000 replicates). Sample regions and accession numbers for the EMBL sequence database are given in brackets. Sequences obtained in this study are marked with asterisk, all others are from the EMBL database. The alignment is available at ftp://ftp.ebi.ac.uk/pub/databases/embl/align/ALIGN_001259.dat.

(C) *Tridacna* spawning frequency (percentage of individuals with gonads featuring empty egg sacs, cf. Experimental Procedures) and sea-surface temperature (courtesy A. Genin, Interuniversity Institute, Eilat) between 2003 and 2004 in the northern Gulf of Aqaba.

Diagnosis

The main diagnostic features that separate *Tridacna costata* from its sympatric congeners are the 5–7 pronounced rib-like vertical folds on the shells' dorsal margin and the prominent wart-like protrusions on the mantle tissue (Figure 4). These features are conservatively present even in small clams <10 cm shell length (L). We found two diagnostic sites (one substitution and one indel) in 103 variable sites of a 415 bp fragment from the mitochondrial 16S rRNA gene. A detailed description of the shells and soft body parts and a revised classification key is in preparation to be published elsewhere.

Experimental Procedures

Sampling, PCR, and Sequencing

Tissue samples of *T. costata* were collected at the Jordanian and Egyptian Red Sea coast (Figure 3A). For comparison, samples of *T. maxima* and *T. squamosa*, which have a sympatric distribution with *T. costata*, were also taken in the Red Sea as well as Indonesia. Additional tissues of *T. crocea* and *H. hippopus* were collected in Indonesia. Tissue samples were taken by cutting ~1 cm² mantle clips from live specimens, preserved in absolute ethanol, and stored at 4°C. This is a method that ensures the

survival of the animal. Genomic DNA was isolated with the Chelex method [33]. Amplification of the mitochondrial 16S rRNA gene (16S) was conducted with the primers 16sar-L (5'-CGC CTG TTT ATC AAA AAC AT-3') and 16sbr-H (5'-CCG GTC TGA ACT CAG ATC ACG T-3'), following the protocol of Schneider and Ó Foighil (1999) [17]. The variable domains D1 and D2 of the nuclear gene encoding ribosomal 28S rRNA from *Symbiodinium* were amplified with the primers 5'-CCT CAG TAA TGG CGA ATG AAC A-3' (forward) and 5'-CCT TGG TCC GTG TTT CAA GA-3' (reverse), with the experimental condition described in Loh et al. 2001 [34]. Both strands were sequenced with the corresponding primers mentioned before with the BigDye Terminator Cycle Sequencing Kit and an ABI automated sequencer according to the manufacturer's recommendations. Editing of sequences was conducted with the program SeqMan (ver. 4.05, DNASTar) and multiple alignment was done with ClustalW [35] as implemented in the software Bio-Edit (ver. 7.0.4.1) [36].

Underwater Surveys

Abundances were determined by carrying out triplicate belt transects (5 m width) surveyed on the reef top and reef edge (<2 m depth, by swimming along predetermined distances [37] (50 m) or, in the case of very low densities, by swimming for predetermined periods of time at a constant speed. Intercalibration ($n = 51$ surveys) showed good correspondence between the two methods (t test for dependent samples, $p = 0.79$), with a survey time of 7 ± 1.2 (SD) minutes corresponding to an area of 250 ± 43 (SD) m².

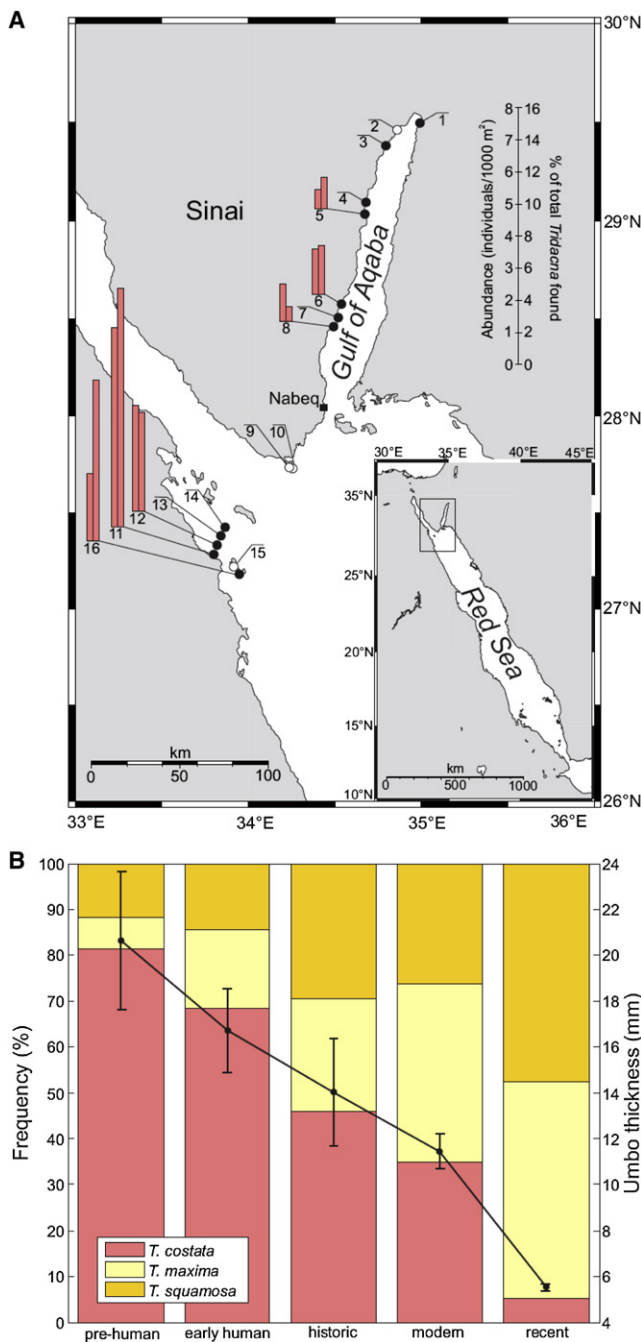


Figure 3. Regional and Temporal Distribution of Red Sea Giant Clams
(A) Map of the northern Red Sea, indicating survey sites with abundance of *Tridacna costata* and its contribution to the three *Tridacna* species. 1, Aqaba; 2–3, Taba; 4–5, Nuweiba; 6–8, Dahab; 9–10, Ras Mohammed; 11–16, Hurghada. Open circles, no empty shells found; filled circles, empty shells found. In the type locality Aqaba, *T. costata* was so scarce that abundances were below detection by either method.
(B) Species composition (stacked bars) and mean size (umbo thickness \pm SEM, line) of *Tridacna* in various stages of human occupation of the Red Sea (pooled data from Aqaba and Nabeq). Prehuman, shell finds from the upper emerged fossil reef terraces corresponding to the penultimate and earlier interglacials [25, 39]; early human, finds from emerged fossil reef terraces corresponding to the last interglacial 115,000 to 135,000 years ago [9, 25–27, 39]; historic, finds from a half-buried campsite >200 m from the present water line in Nabeq; modern, shells along surf deposits; recent, freshly discarded shells at Bedouin campsites (see Supplemental Data). Between

In sites where no transects were laid, the survey time spent (sandy patches excluded) was converted to area for the calculation of clam densities.

Land Surveys

The composition and abundance of shells was assessed along the shores and in emerged reef terraces of Aqaba and Nabeq. Sampling positions and elevation above sea level (m above sea level [a.s.l.]) were determined by GPS and documented by video and photographs. Reef terraces investigated were dated according to previous studies, by using the positions, elevations, and line drawings reported from these sites [25, 38] as well as photographs (Figures S4 and S5). We used the following categories: prehuman, reef terraces 8–33 m a.s.l. (likely MIS7, 9, and 11 [25, 39]) prior to the Red Sea occupation by anatomically modern humans [9]; early human, reef terraces 4–9 m a.s.l. from the last interglacial [26, 27], corresponding to the early Red Sea occupation by anatomically modern humans [9]; historic, a ~50 m diameter sandy mound 5 m a.s.l. located away from the shoreline (~200 m distance), corresponding to a long-abandoned Bedouin campsite with half-buried shells of marine molluscs including *Strombus* and *Tridacna*; modern, a mix between old and new shells collected from flats along the shore (0–2 m a.s.l.); and recent, recently discarded shells at presently used Bedouin boat launch sites (<1 m a.s.l.). *Tridacna* shells were collected and identified and shell lengths (intact shells only) and umbo thickness (shells and fragments) were measured to the nearest mm.

Spawning Frequency

Giant clams are hermaphroditic, protandric females. In situ gonad biopsy [40] was carried out on the same set of wild clams at the Aqaba Marine Science Station between March 2003 and March 2004, between 2 and ~16 m depth: five *T. costata* (27–34 cm shell length [L]), six *T. maxima* (14–26 cm L), and seven *T. squamosa* (23–30 cm L). No actual spawning has been observed during the in situ biopsy or in the field surveys. The following egg developmental stages were used: early, mature, regressive, and spawning (empty egg sac without eggs) [40], and the mean frequency distribution of the different stages was determined by using triplicate random counts (each n = 30 eggs).

Length, Weight, and Fecundity

In order to be able to include incomplete specimens in the analyses (esp. in the case of fossil shells), giant clam size was determined by measuring the thickness of shells at the umbo (U, in mm; see Figure S1). U was converted to giant clam biomass (B, in g tissue dry mass) and fecundity (F) by using linear relationships between U and shell length (L) determined on whole shells in our surveys ($L = 7.7 \times U + 57.4$, $r^2 = 0.71$, $n = 212$), and published B to L and F to L relations established for the subgenus *Chametrachea*, according to $B = (1.17 \times 10^{-7}) \times L^{3.65}$ [41] and $F = 0.0074 \times L^{4.03}$ [42].

Accession Numbers

16S rDNA sequences of giant clams (*Tridacna* spp) have been deposited in the EMBL (European Molecular Biological Laboratory) sequence data base under accession numbers AM909726–AM909765.

28S rDNA sequences of zooxanthellae (*Symbiodinium*) have been deposited in the EMBL sequence data base under accession numbers FM164856–FM164883.

Supplemental Data

Supplemental Data include Supplemental Results, five figures, and two tables and can be found with this article online at <http://www.current-biology.com/cgi/content/full/18/17/1349/DC1/>.

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43 and 482 shells were identified for each age interval yielding a total n = 955 shells and shell fragments, of which n = 437 shells could be measured.

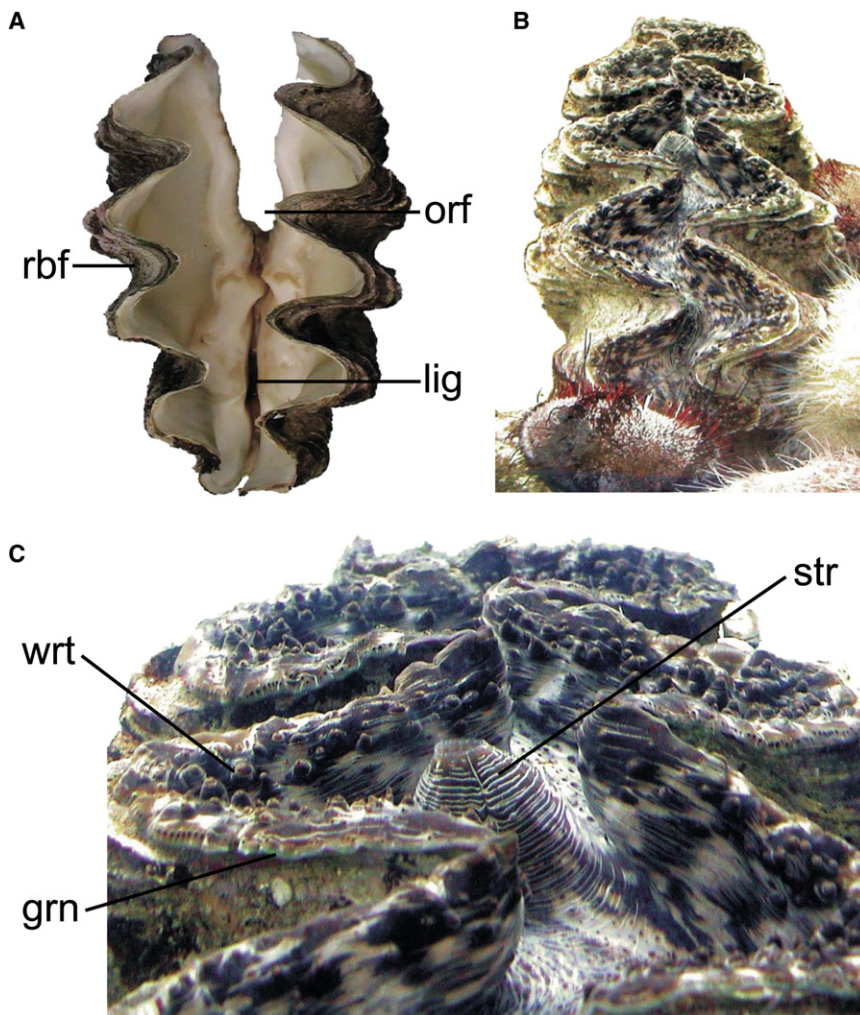


Figure 4. External Morphology of *Tridacna costata*

Holotype specimen of *Tridacna costata* in dorsal view (length, height, width: 32.0, 19.6, 17.2 cm). External morphology follows the anatomical orientation of giant clams [15, 43, 44] (see Figure S1).

(A) The distinguishing deep rib-like folds resulting in a zig-zag dorsal shell margin.

(B) The most common subdued brown mottled mantle pattern and the shell.

(C) The green mantle margins, "wart-like" protrusions, and pale striations following mantle contour.

Abbreviations: wrt, warts; str, striations; gm, green margins; rbf, riblike folds; lig, hinge ligament; orf, orifice. Photos by Y. Ahmed.

the photographs for Figures 1 and 4, respectively; A. Genin for providing the temperature data in Figure 2; J. Lucas for taxonomic advice; T. Felis for advice in the identification of the fossil terraces; J. Lucas, A. Genin, V. Ittekkot, V. Smetacek, and T. Felis for reviewing earlier versions; two anonymous reviewers for improving the final manuscript; and the directors and staff of the Aqaba Marine Science Station, Center for Tropical Marine Ecology, and Alfred-Wegener-Institute for support.

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